

# LIFE HISTORIES OF SPECIES IN THE *PARDOSA PULLATA* GROUP, A STUDY OF TEN POPULATIONS IN THE NETHERLANDS (ARANEAE, LYCOSIDAE)

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## ABSTRACT

The phenology of several populations of the *Pardosa pullata* group — *P. prativaga* (L. Koch), *P. prativaga* var. *fulvipes* (Collett) and *P. pullata* (Clerck) — in the Netherlands was studied in 1969 and 1970. The results are discussed in the context of the habitats of the respective species, the classification of the *P. pullata* group, as well as in the context of the possibility of hybridization in mixed populations.

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## I. INTRODUCTION

In the *Pardosa pullata* group the species *Pardosa prativaga* (L. Koch, 1870) (including *P. prativaga* var. *fulvipes* (Collett, 1875)) and *P. pullata* (Clerck, 1757) are distinguished. The species differ in the annulation and spinosity of the legs to a fairly large extent (Wiebes, 1959). However, the general morphology suggests a very close relationship. Comparison of several populations showed that within either species morphological differences exist between samples from pure and those from mixed populations. These data and the observation of specimens intermediate between *P. pullata* and *P. prativaga* in the field suggest that hybridization may occur (Locket & Millidge, 1951; Den Hollander, 1970).

In this paper the phenology of the species mentioned above is dealt with. The results are discussed in the context of the habitats of the species, the systematic relationships and the possibility of hybridization between the species. Studies concerning physiological and ethological barriers, as well as niche differentiation are in progress.

The life-history of the species of the *P. pullata* group is of the common *Pardosa* type (Wiebes, 1960; Vlijm, Kessler & Richter, 1963; Vlijm & Kessler-Geschiere, 1967). In early spring only juvenile spiders occur. Within a few weeks after the appearance of the first adults the numbers of males and females without cocoon reach a maximum. Probably during this period mating occurs (Tretzel, 1954; Wiebes, 1960). The first females with cocoon appear in the same period. Pulli emerge from the cocoons after about 4 weeks; they stay 1—3 days upon the abdomen of the female.

In the beginning of June the numbers of adult males decrease. The number of females decreases in late summer. Simultaneously the numbers of juveniles increase. These juveniles overwinter.

## II. MATERIAL AND METHODS

The *P. pullata* group is considered separated into three subgroups: the *pullata*, *prativaga* and *fulvipes* subgroups (Den Hollander, 1970).

Ten populations in the Netherlands (Table 1) were sampled with a frequency of about once per ten days, from April to October, in 1969 and 1970. Each sample was obtained by collecting any visible spider by hand during a 20 min. period. Thus catch size will depend on such factors as the structure of the habitat, the developmental stage of the spider and the weather conditions.

Measurements of the cephalothorax length (i.e. the distance between the posterior lobes of the cephalothorax and the anterior margin of the posterior median eyes, cf. Den Hollander, 1970), were used to study the succession in time of the larval instars. Measurements in micrometer units (1 MU = 0.042) were obtained with a Reichert Stereomicroscope at a magnification of  $6.3 \times 4$  (accuracy 2.3%). When taking the measurements, the anterior margin of the eyes and the posterior lobes of the cephalothorax were brought in focus simultaneously.

The period of carrying pulli is short in relation to the period between the successive samples, so that the chances of catching females carrying pulli are small. Consequently, only few of them were caught. Therefore data on this stage are not included.

## III. RESULTS

## 1. Changes in population structure during the year

## A. General differences between the subgroups

Table II presents mean numbers per sample of juveniles, adult males and females (the latter without cocoon, indicated as ♀ ♀, or with cocoon, indicated as ♀ ♀ c), for the three subgroups separately.

## a. Adults

Comparison of the phenological characteristics of the three subgroups gives the following results. Differences occurred as to the period of the final moult in the three subgroups (*pullata*: 4''/4'''; *fulvipes*: 5'; *prativaga*: 5''; 4', 4'', 4''' stand for first, second and third decades of April, respectively). In each subgroup adult males were found about one week earlier than females. The highest numbers of males occurred in May. However, in the subgroup *pullata* males were also present in April and, in smaller numbers, in June and July. High numbers of males occurred in the *fulvipes* subgroup in both May and June. Males of the *prativaga* subgroup generally were found only during May.

The numbers of females without cocoon (♀ ♀) were highest in May in the subgroups *pullata* and *prativaga*. In the *fulvipes* subgroup large numbers of ♀ ♀ occurred in May, but also in June and July. Small numbers of ♀ ♀ occurred in June in the subgroups *pullata* and *prativaga*, and in August and September in the subgroup *fulvipes*. Thus in May the numbers of both ♂ ♂ and ♀ ♀ were highest. This indicates that the period of copulation then occurs. With respect to this period rather slight differences existed between the three subgroups (*pullata*: 5'/''; *fulvipes*: 5''/'''; *prativaga*: 5''').

Table I. The localities of the studied populations of the *P. pullata* group

Locality	Code	Species
Vogelenzang, Heemstede	VZ	<i>P. prativaga</i>
Groene Punt, Oostvoorne	GP	<i>P. prativaga</i>
Lange Pad, Oostvoorne	LP	<i>P. prativaga</i>
Bosweitje, Rockanje	BW	<i>P. prativaga</i> , <i>P. pullata</i>
Amstelveense Poel, Bovenkerk	AP	<i>P. pullata</i>
Hollandse Rading, Hilversum	HR	<i>P. pullata</i>
Arnica-weitje, Schiermonnikoog	Sch	<i>P. pullata</i>
de Eese, Steenwijk	E	<i>P. prativaga</i> var. <i>fulvipes</i>
de Woldberg, Steenwijk	S	<i>P. prativaga</i> var. <i>fulvipes</i>

Females carrying cocoons (♀ ♀ c) appeared in the middle of May (5'') in the *pullata* subgroup. In the subgroups *prativaga* and *fulvipes* they appeared in the beginning of June (6'). Thus the egg maturing period (i.e. the period between the appearance of the first ♀ ♀ and that of the first ♀ ♀ c) was different in the three subgroups (*prativaga*: 10—20 days; *fulvipes* and *pullata*: 20—30 days).

In all three subgroups the numbers of ♀ ♀ c were highest in June. However, in the subgroup *pullata* ♀ ♀ c occurred already in May and in the *fulvipes* subgroup large numbers of ♀ ♀ c were found not only in June, but also in July and August. In the *prativaga* subgroup they hardly occurred outside June. After the periods of peak num-

bers only small numbers of ♀ ♀ c were found in July (*prativaga*), in July and August (*pullata*) and in September (*fulvipes*).

The first pulli emerged from the cocoons in the period between the middle of June and the beginning of July. Again some differences existed between the subgroups (*pullata*: 6''/7'''; *prativaga* and *fulvipes*: 6'''/7'). Thus in the subgroups *prativaga* and *fulvipes* females carry their egg sacs during a period of 20—30 days. The length of this period seems to be longer in the subgroup *pullata* (30—40 days).

In the subgroup *prativaga* adult females hardly occurred after the emergence of the pulli. This means that females of this subgroup produced a cocoon only once. Probably they die after the emergence of the pulli. Adult females did occur in the subgroups *pullata* and *fulvipes* in that period. However, in the *pullata* subgroup their numbers were low, as compared with those in May and June. The *fulvipes* females occurred in comparable numbers both before and after the emergence of the pulli. For the subgroups *pullata* and *fulvipes* more information comes from comparing the numbers of females carrying cocoons with those without cocoons (♀ ♀ c/♀ ♀). In the subgroup *pullata* maxima in this ratio occurred in the beginning of June (6') and in the middle of July (7''), respectively. In the *fulvipes* subgroup the first peak occurred in the middle of June (6''), the second one around the end of July (7'''/8'). It may be assumed that the ♀ ♀ c found after the emergence of the first pulli are females which had constructed a cocoon for the second time. Indeed the sampled cocoons in the period just after the emergence of the first pulli were very fresh. Thus the majority of the females in the *pullata* subgroup produced a cocoon only once, as was the case in the *prativaga* subgroup. A smaller part produced a second cocoon (small numbers in July). In the *fulvipes* subgroup large numbers of females with a cocoon could be caught in the respective periods. This indicates that in this subgroup production of a second cocoon is the rule. The small numbers of ♀ ♀ c occurring after the indicated periods in the respective subgroups, viz. in July for *prativaga*, in August for *pullata* and in September for *fulvipes*, probably concerned females which accidentally had lost their cocoon before the pulli emerged and afterwards produced a new one.

#### b. Juveniles

Juvenile spiders also occurred at different times during the year in the three subgroups. Generally their numbers decreased strongly during the period of the final moult. In the subgroups *pullata* and *prativaga* juveniles were nearly absent in the samples after the appearance of the first ♀ ♀ c. In the *fulvipes* subgroup, on the other hand, large numbers of juveniles occurred throughout the whole summer.

In the subgroups *pullata* and *fulvipes* juveniles occurred in large numbers in autumn, as well as in spring. However, *prativaga* juveniles scarcely could be found in the autumn samples. This may be caused by the specific behaviour of these juveniles in relation to habitat (see below).

### B. Population differences within the subgroups

Table III presents the numbers of juveniles, adult males and females (the last without or with cocoon, indicated with ♀ ♀ and ♀ ♀ c, respectively) per sample.

#### a. Subgroup *prativaga*

The phenological data of the different populations of the *prativaga* subgroup were

Table II. The number of juveniles, adult males and females (the last without (♂♂) and with (♀♀) cocoon) per sample, summarized per subgroup for the two years.

	4			5			6			7			8			9			10		
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
<i>subgroup pratvaga</i>																					
juv.	35	32	54	57	26	17	2	1	2	1	.	2	.	.	5	8	15	5	7		
♂♂	-	-	-	1	19	16	4	1	1	-	.	-	.	.	-	-	-	-	-		
♀♀	-	-	-	-	6	19	5	-	2	1	.	-	.	.	1	-	-	-	-		
♀♀c	-	-	-	-	-	2	9	9	8	3	.	2	.	.	-	1	-	-	-		
<i>subgroup fulvipes</i>																					
juv.	19	16	61	47	58	27	26	24	.	42	15	38	26	.	41	.	60	92	63		
♂♂	-	-	1	15	33	12	15	5	.	1	1	-	-	-	-	-	-	-	-		
♀♀	-	-	-	13	28	24	31	9	.	26	15	8	1	.	9	.	5	2	-		
♀♀c	-	-	-	-	-	2	23	39	.	39	31	41	19	.	13	.	6	-	-		
<i>subgroup pullata</i>																					
juv.	35	29	27	19	3	3	1	-	1	1	-	4	5	.	21	44	37	30	33		
♂♂	-	4	12	19	12	20	6	3	2	2	-	1	-	-	-	-	-	-	-		
♀♀	-	1	6	9	13	12	3	4	4	2	1	2	4	.	1	1	-	-	-		
♀♀c	-	-	-	-	6	15	21	15	8	5	9	6	3	.	3	1	-	-	-		



Table III. The numbers of juveniles, adult males and females (the last without (♀♀) and with (♀♀c) cocoon) per sample for each population in 1969 and 1970, respectively; a: subgroup *pratnaga*; b: subgroup *pullata*; c: subgroup *fulvipes*.

Table IIIb

subgroup <i>pullata</i>			April			May			June			July			August			September			Okt.
population			I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	
HR	Juv.	30 24	29	8	15 60	5	-	6	-	2	-	-	-	-	-	-	-	-	-	-	I
	♂♂	-	-	8	- 18	21	-	14 15	44 18	9 5	2 2	3	-	-	-	-	-	-	-	-	38
	♀♀	-	-	1	- 6	15	-	12 4	10 18	2 1	-	1	-	-	-	-	-	-	-	-	-
	♀♀c	-	-	-	-	-	-	14	- 27 11	29 10	7 24	7	-	-	-	-	-	-	-	-	-
BW	Juv.	43 32	19	-	- 31	12 21	2	-	3 3	1 4	1	-	1	-	-	-	-	-	-	-	48
	♂♂	-	1 14	-	- 26	21 17	12 16	10 18	7 6	3 1	4	-	-	-	-	-	-	-	-	-	-
	♀♀	-	-	5	- 10	9 7	18 28	7 11	2 5	1 1	14	-	-	-	-	-	-	-	-	-	-
	♀♀c	-	-	-	-	-	-	8 18	19 22	18 27	20 2	9	-	-	-	-	-	-	-	-	-
Sch	Juv.	-	60	29 86	27 42	46 19	-	8 7	2	-	1	-	1	-	-	-	-	-	-	-	36
	♂♂	-	-	4	- 25 9	33 25	-	10 12	19	12 4	5	-	-	-	-	-	-	-	-	-	-
	♀♀	-	-	1	- 15 6	13 11	-	17 5	21	2 5	13 2	3	-	-	1	6	-	-	-	-	-
	♀♀c	-	-	-	-	-	-	-	7 3	33 16	25 8	11	-	8	9	9	3	-	-	-	-
AP	Juv.	18 43	6 13	6 15	-	6 11	-	3 1	-	-	-	-	1	-	-	-	-	-	-	-	10
	♂♂	-	-	-	- 2	8 6	5 11	8 6	1	-	1 3	-	-	-	-	-	-	-	-	-	-
	♀♀	-	-	-	-	5 4	7 9	15 5	1	-	4 2	-	-	1	-	-	-	-	-	-	-
	♀♀c	-	-	-	-	-	-	2	-	10 17	10	-	17 12	-	-	-	-	-	-	-	-







very similar. Small differences were found between the successive years. In 1970 ♀ ♀ c occurred about 10 days earlier (5''') than in 1969 (6'). In all the populations of the *pratīvaga* subgroup more adult females occurred after the emergence of the first pulli from the cocoons (July) in 1970 than in 1969. In the former year probably a relatively small proportion of these females produced a second cocoon.

#### b. Subgroup *fulvipes*

The phenological data are rather similar in the different *fulvipes* populations. In population E adults occurred somewhat earlier (4''') than in population S (5'). In the former females produced their cocoon about ten days ahead of population S (5''' and 6', respectively). These differences existed in both years although they were less conspicuous in 1970 than in 1969.

#### c. Subgroup *pullata*

The phenological data of the populations of the *pullata* subgroup were rather different from each other, as compared with those of the subgroups *pratīvaga* and *fulvipes*. This was especially true in 1970. The differences concern the time of the final moult, the length of the egg maturing period, the time of cocoon construction and the length of the period when males occur in the populations. In 1969 the phenological data of the populathions HR, BW and Sch were similar. In population AP both males and females became adult 10—20 days later (4''' and 5', respectively) than in the other populations (4''). In all populations ♀ ♀ c appeared in the same period (5''). Thus the length of the egg maturing period varied from 10 (AP) to 30 days (HR, BW, Sch). The number of males decreased strongly in the beginning of June (6') in the respective populations. This means that the length of the period that males occurred in large numbers in the populations varied from 40 (AP) to 50 days (HR, BW, Sch).

In 1970 the phenological data of population BW were comparable with those in 1969. However, in the other populations the first adults appeared 10—30 days later than in the former one (Sch: 10 days; AP: 20 days; HR: 30 days). Obviously the time of the final moult in 1970 occurred 0—30 days later than that in 1969 in the respective days (BW: 0 days; AP: 0—10 days; Sch: 10 days; HR: 30 days).

Again in 1970 the numbers of males decreased strongly in the same period as in 1969 in all populations (6'). As males became adult rather late in some populations, the length of the period that males occurred in the populations varied in 1970 from 20—50 days (HR: 20 days; AP: 30 days; Sch: 40 days, BW: 50 days).

As opposed to females in population BW, those in the populations HR, Sch and AP constructed their cocoons in 1970 ten days later than in 1969 (5'' and 5''', respectively). Thus the length of the egg maturing period varied in 1970 from 10—30 days (HR: 10 days; BK: 20 days; Sch: 30 days; BW: 30 days).

In 1970, as compared with 1969, the numbers of ♀ ♀ c were larger in the July and August samples. This was especially clear in the population HR. As in the *pratīvaga* subgroup, more females probably produced a second cocoon in the former year.

From the above data the following conclusions can be drawn. The time of the final moult is variable within the *pullata* subgroup. Variations occur between different populations in one year, as well as in one population between successive years. However, construction of cocoons and disappearance of males from the populations occur about in the same period in all populations in the two successive years. Thus especially the

length of the egg maturing period (10—30 days) as well as the length of the period that males occur in the populations (20—50 days) varies. The later the final moult occurs in spring the shorter both periods are. In this respect the subgroup *pullata* differs clearly from the subgroups *pratavaga* and *fulvipes*. The final moult in the latter two subgroups normally occurs in late spring (5', 5''). The length of the egg maturing period in these subgroups (10—20, and 20—30 days, respectively) equals that of the period in those *pullata* populations, in which the final moult also occurs in late spring. The same holds for the period that males occur in the populations in large numbers (*pratavaga*: 20 days; *fulvipes*: 20—40 days; *pullata*: 20—50 days).

### C. The number of eggs per cocoon

Table IV gives the mean number of eggs per cocoon for the respective populations  
 Table IV. The mean number of eggs per cocoon in *P. pullata*. The numbers are given per population (at different times during the breeding season) for 1969 and 1970, respectively  
 (a: subgroup *pratavaga*; b: subgroup *pullata*; c: subgroup *fulvipes*).

#### a: subgroup *pratavaga*

population	data	number of cocoons	variation	mean number of eggs
VZ	4/6; 15/6-16/6	32, 12	31-72, 27-50	52, 42
BW	2/6-26/6; 28/5- 5/6	33, 24	32-72, 25-70	52, 47
LP	19/6-26/6; 5/6-30/6	20, 16	(32-63)	49, 45
GP	2/6- 9/6; 5/6	10, 13	29-52, 40-70	46, 48

#### b: subgroup *pullata*

HR	4/6; 26/5	27, 18	22-39, 22-40	31, 29
	29/7	18	8-27	18
BW	23/5- 2/6; 22/5	33, 22	23-56, 30-54	37, 39
	28/7; 30/6	11, 13	10-40, 12-39	26, 27
Sch	5/6; 19/6	33, 16	21-44, 14-39	30, 26
	23/7-30/7	18	7-33	19
AP	22/5- 5/6; 26/5	26, 27	22-62, 30-54	44, 41

#### c: subgroup *fulvipes*

S	6/6-13/6; 16/6	26, 36	20-47, 15-49	32, 31
	1/8; 13/7	23, 30	8-29, 9-48	19, 22
	24/8	10	4-16	11
E	6/6-13/6; 16/6	26, 25	24-54, 19-45	33, 31
	13/7	22, 22	10-25, 7-27	17, 18
	1/8; 24/8	10	7-17	12

and the successive years. The egg sacs were taken from samples in June, July and August.

Obviously the largest numbers of eggs per cocoon occurred in the subgroup *prativaga*, the smallest numbers were found in the *fulvipes* subgroup in the cocoons sampled in August. The numbers of eggs in the cocoons of the *pullata* subgroup (sampled in June and July) were slightly higher than in the *fulvipes* subgroup. The numbers in the July egg sacs were about 30–40% lower than those in the June egg sacs. Again 30–40% less eggs were found in the August cocoons than in the July cocoons. Thus it seems likely that in those populations of the *pullata* subgroup in which cocoons can be found during July, these cocoons represent second cocoons. In the same way, cocoons found in the populations of the *fulvipes* subgroup during July and August represent second and third cocoons, respectively.

The mean number of eggs per cocoon differs only little between the two populations of the subgroup *fulvipes*. The differences between the four populations of the subgroup *prativaga* were also small, although some differences existed between the numbers of eggs per cocoon in the successive years, particularly in the population VZ. Rather large differences occurred between the populations of the *pullata* subgroup. The egg sacs in the populations BW and AP contained a larger (30%) number of eggs than those in the populations HR and Sch.

Although the smallest numbers of eggs per cocoon occurred in the *fulvipes* subgroup, these females produced the largest numbers of offspring. All females produced two egg batches and 40% produced a third one. Thus the total number of eggs produced by 100 females amounts to about 5500. In the *prativaga* subgroup the females produced a cocoon only once and the total number of eggs produced by 100 females thus amounts to about 4700. Only 40% of the females in the *pullata* subgroup produced a second cocoon. The total number of eggs produced by 100 females in this subgroup thus amounts to about 4400, the smallest number as compared with that in the subgroups *prativaga* and *fulvipes*.

Concerning these figures, however, it must be taken into account that not all eggs in an egg batch develop to pulli, because parasites may destroy some of the eggs in a cocoon (Kessler, personal communication).

#### D. Conclusions

The final moult occurs earlier in the *pullata* subgroup (April) than in the subgroups *prativaga* and *fulvipes* (May). However, the time of the final moult is variable within the *pullata* subgroup both between populations and successive years. On the other hand cocoon production, as well as the disappearance of males from the populations, occur in the three subgroups about in the same period (the second half of May and the beginning of June, respectively). As a consequence the length of the egg maturing period, as well as the length of the period that males occur in the populations, is longer and more variable in the *pullata* subgroup than in the subgroups *prativaga* and *fulvipes*. The mean number of eggs per cocoon is largest in the *prativaga* subgroup and smallest in the *fulvipes* subgroup. This number decreases in the successive cocoons which are produced during the breeding season. Rather small differences exist between the successive years. The differences between the populations in the *pullata* subgroup are larger than those in the other subgroups.

On the basis of the occurrence of adult females with and without cocoons, as well as

the numbers of eggs per cocoon at different times during the breeding season, it is concluded that females in the *prativaga* subgroup produce a cocoon only once. Females in the *pullata* subgroup would produce once or twice a cocoon (variable per population and per year). Females in the *fulvipes* subgroup normally produce an egg batch two or three times in succession.

## 2. Growth of juvenile spiders

In the previous section the assumption was made that females in the subgroup of *prativaga* generally produced a cocoon only once, though in 1970 a minority of the females may have produced a second one. In general a minor part of the females in the *pullata* subgroup produced a cocoon twice, whereas in the subgroup *fulvipes* all females normally produced two cocoons. To obtain more evidence on this point the cephalothorax length of the juveniles from the autumn and spring samples was measured. Graph 1 represents the frequency distributions of the cephalothorax length of juveniles in the respective samples.

It is assumed that every part of a polymodal frequency distribution (when it occurs consistently both in autumn and in spring) will represent juveniles emerging from cocoons produced in different periods of the breeding season. The number of larval instars of the concerned species is unknown. This number is rather variable even at the species level and seems to be dependent on environmental factors (Browning, 1941; Levy, 1970).

Generally, spiders moult three times during the larval stage and five to ten times during the nymphal stage (Holm, 1940; Juberthie, 1955; Vachon, 1957). In this study the successive larval instars as defined by cephalothorax lengths are presented by a graph indicating the number of moults, which will occur before the adult stage is reached (e.g., adults: stage A; subadults: stage A-1 etc.). Subadults in the three subgroups clearly show sexual dimorphism. As the spiders were collected by hand only juveniles of the later larval instars occurred in the samples.

Graph 1 shows that the cephalothorax lengths of juveniles in the corresponding stages are about the same in the three subgroups (stage A-1: 55 MU; stage A-2: 47 MU; stage A-3: 40 MU; stage A-4: 33 MU). Increase in cephalothorax length in the successive instars thus amounted to 7—8 MU. Pulli emerging from the cocoons showed cephalothorax lengths of about 20 MU. Thus it is plausible that the cephalothorax length of stage A-5 juveniles (which were not represented in the samples) amounts to about 26 MU and that pulli emerging from the cocoons correspond to stage A-6 juveniles (20 MU). In all the three subgroups pulli emerging from the cocoons will moult six times before the adult stage is reached.

### A. Subgroup *prativaga*

In general juveniles in this subgroup show unimodal cephalothorax lengths in all samples (Graph 1a). This means that these juveniles will have emerged from the cocoons in the same period. In the autumn the juveniles have grown to stage A-2, i.e., four moults occurred after the emergence from the cocoons. These juveniles overwinter. Next spring they moult to subadults and afterwards the final moult occurs.

Especially in the autumn of 1970 small juveniles occurred in the samples from the populations BW and LP. These juveniles may have emerged from second cocoons produced by some females in these populations (see above).



Pulli emerged from the first cocoons in the beginning of July and from the second ones in the beginning of August. During September the juveniles from the first cocoons moult to stage A-2, those from the second cocoons to stage A-3. Thus four moults after emergence from the cocoons take 2—3 months, while three moults take 1—2 months.

### B. Subgroup *pullata*

In general the frequency distributions of the cephalothorax length are bimodal (Graph 1b). The respective length classes in the autumn and spring samples represent stage A-2 and stage A-1 (subadult) juveniles. The bimodality of the distributions is very clear in the populations BW and Sch in 1969 and 1970. This suggests that in these populations the juveniles which occurred in autumn emerged from cocoons in different periods of the breeding season (stage A-1 from first cocoons in June, stage A-2 from second cocoons in July). After overwintering stage A-1 juveniles moulted to the adult stage, stage A-2 juveniles moulted to the subadult stage and adult stage, successively.

However, differences exist between the respective populations and between the successive years. In spring 1969 the juveniles of population HR showed uniform cephalothorax lengths (subadult). The same holds for juveniles collected in autumn 1969 and in spring 1970. It may be concluded that in this population, in both the breeding seasons 1968 and 1969, females produced a cocoon only once. On the other hand, in the autumn of 1970 juveniles of two length classes occurred in the samples. Therefore, in this breeding season at least part of the females evidently produced a second cocoon. The same, though to a lesser extent, is true for the population AP.

The last moult of juveniles before overwintering occurs during September in the *pullata* subgroup. Dependent on emergence from first (the middle of June) or second (the end of July) cocoons this moult represents the fifth or fourth moult after the emergence of pulli, respectively. Thus the developmental time from pulli (probably stage A-6) to subadult (stage A-1) takes 3 months, that from pulli (A-6) to stage A-2 juveniles 1—2 months. This means that the duration of the successive larval instars of juveniles in the *pullata* subgroup is shorter than that of juveniles in the subgroup *pratīvaga*.

### C. Subgroup *fulvipes*

The growth of juveniles in the *fulvipes* subgroup is rather more complex. First, juveniles occur during the whole breeding season and secondly, the frequency distributions of cephalothorax lengths are polymodal (Fig. 1c). In late summer and autumn (August-October) three length classes could be clearly distinguished. Most juveniles occurred in the class of the largest cephalothorax lengths (stage A-1, subadult), but also stage A-2 and stage A-3 occurred. In spring juveniles of the same three length classes occurred. In summer (June-August) juveniles of various cephalothorax lengths were found but they could be classed mainly in stage A-2 and stage A-3.

It is suggested that this rather complex picture may result from the fact that females in the *fulvipes* subgroup produce two or three cocoons successively. After the breeding season stage A-3 juveniles appeared in the samples at the end of August. These juveniles will have emerged from first cocoons in the beginning of July. They moult to stage A-2 juveniles in September and in this stage they overwinter. In spring these juveniles moult to subadult (stage A-1) and then to adult. The life history of these juveniles thus

closely corresponds to that of the *prativaga* subgroup. The developmental time from the pulli stage (stage A-6) to the fourth moult afterwards (stage A-2) also amounts to 2—3 months.

However, at the same time stage A-3 juveniles still occurred in September. These juveniles will have emerged from second cocoons around the end of July. They overwinter in stage A-3 and moult to stage A-2 next spring. In this stage they are found during the breeding season. In August moulting to subadult (stage A-1) occurs, then they overwinter for a second time. Next spring the final moult occurs. The developmental time of these juveniles from pulli to the third moult afterwards (stage A-3) amounts to 1—2 months, as was the case in the *prativaga* subgroup.

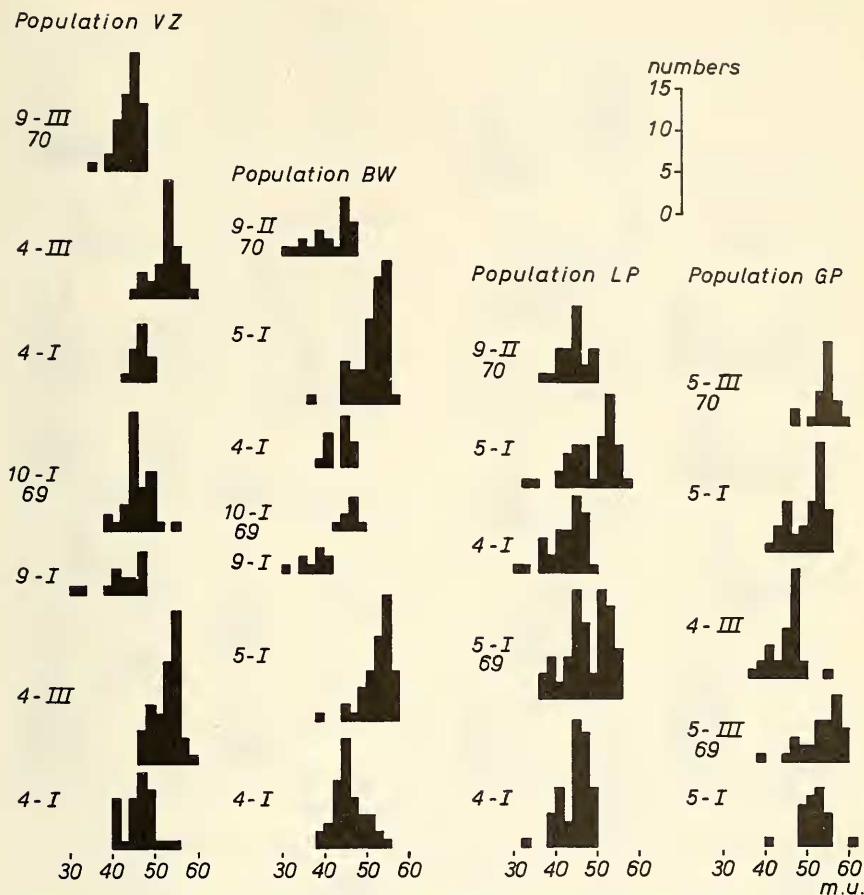
During May stage A-3 juveniles again appeared in the samples. These juveniles will have emerged from third cocoons (in September). They may have overwintered as stage A-4 juveniles and moulted to stage A-3 in spring. During July and August these juveniles moult once (stage A-2) and again to become subadult (stage A-1). After overwintering the final moult occurs next spring. As a result of this specific life history of pulli emerging from second and third cocoons juveniles occur in the populations throughout the breeding season.

Concerning these juveniles an interesting phenomenon was found in the population E during the breeding season 1970. In June 1970 rather large numbers of subadults (stage A-1) were found which showed the abnormality of excessively large cephalothorax lengths. These lengths even exceeded that of adults. These anomalies may be caused by disturbancy of endocrine processes. A period of low temperatures seems to be essential in controlling the endocrine processes which regulate the final moult in spiders (unpublished results from the department). Probably the chain of these processes was disturbed by the exceptionally warm and sunny weather during October 1969 (about 27° C and 5% above normal, respectively).

The fact, that *fulvipes* juveniles which emerge from second and third cocoons do not moult after the first overwintering, suggests that the developmental stage during which the period of low temperatures occurs is important. The above data show that only when overwintering occurs in the last two instars (stage A-2 and stage A-1) before the adult stage, the final moult takes place next spring.

#### D. Conclusions

A comparison of the growth of juveniles in the three subgroups gives the following results. The number of larval instars after the emergence of pulli from the cocoons appears to be the same in the three subgroups. However, the duration of the successive larval instars (before overwintering) is shorter in the subgroup *pullata* than in both the subgroups *prativaga* and *fulvipes*. In all three subgroups the last moult before overwintering occurs in September, the first moult after overwintering in April (Graph 2). The stage in which instars overwinter differs between the subgroups. In the subgroup *prativaga* juveniles overwinter in the instar before the subadult stage (stage A-2). Juveniles in the *pullata* subgroup overwinter in stage A-2 as well as in the subadult stage (stage A-1). Juveniles in the subgroup *fulvipes* overwinter in the last four instars (stage A-4, A-3, A-2 and A-1). These differences can be understood as a result of differences in the duration of the successive larval instars as well as in the time of emergence from the cocoons (first, second or third cocoons). The measurements of cephalothorax length of juveniles confirm the conclusions stated in the previous section. Females in the sub-



Graph 1a. The frequency distributions of the cephalothorax length of juveniles during the year. Subgroup *prativaga*

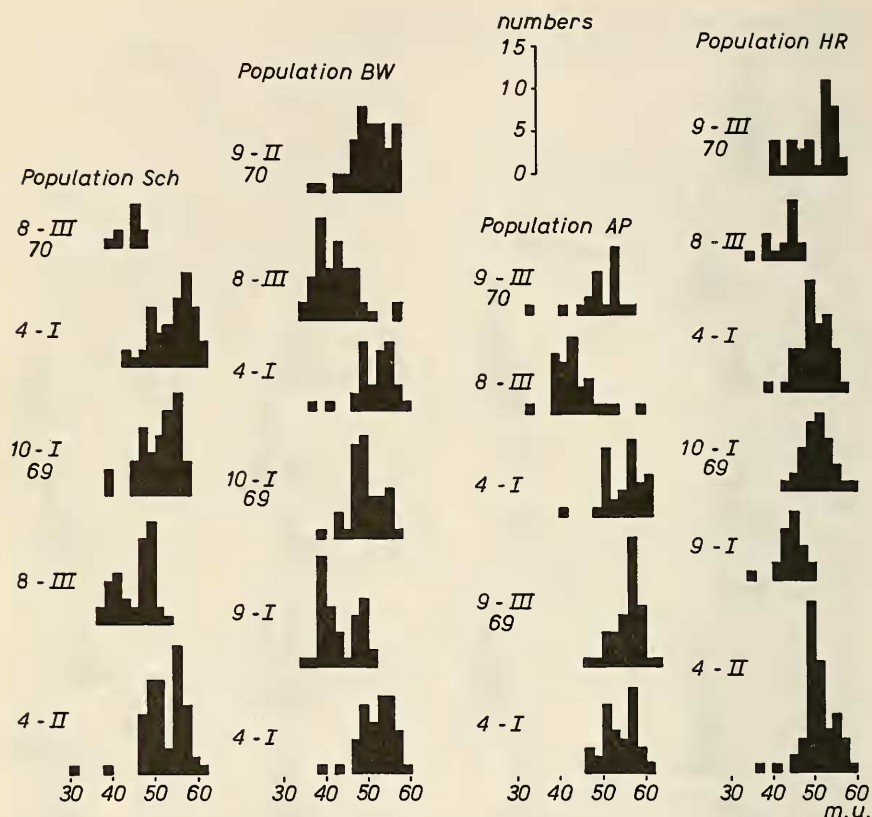
group *prativaga* normally produce a cocoon only once. Those in the *pullata* subgroup produce a cocoon once or twice dependent on the population and the year. In the subgroup *fulvipes* females normally produce two cocoons and part of the females produce a third one.

### 3. The habitats of the studied populations

#### A. Description

The general features of the habitats of *Pardosa* species have been described e.g. by Dahl (1908), Locket & Millidge (1951) and Wiebes (1959). According to these authors *P. prativaga* occurs in fields and marshy soils with a rather dense growth of high grasses and other plants. *P. pullata* would occur in the same localities but also



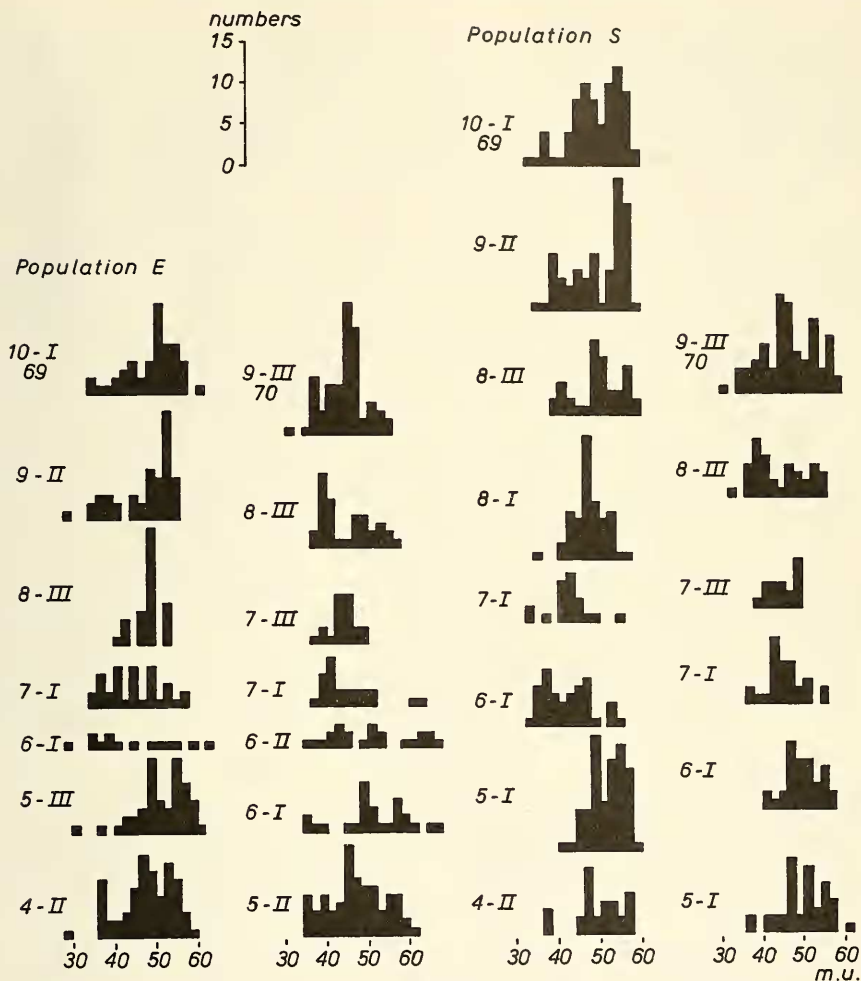


Graph 1b. The frequency distributions of the cephalothorax length of juveniles during the year.  
Subgroup *pullata*

in more dry places. A densely structured low vegetation, e.g. a moss carpet, will mostly be present. *P. prativaga fulvipes*, as far as we know for the Netherlands, is restricted to fens, grown with *Sphagnum*.

It is evident that the structure of the vegetation influences the temperature in this vegetation. Temperature is important for the life history of spiders, especially for the time of the final moult, the length of the egg maturing period and the development of juveniles (see above, and Jones, 1941). Temperature in the places where the spiders are found depends on weather conditions, exposure of the habitat and the structure of the vegetation. Observations concerning these features have been made during the sampling periods in the populations of the *P. pullata* group (Table 1, on p. 257).

The populations LP, BW and GP occur in marshy valleys on the border of calcareous dunes. The field LP (*prativaga*) is sheltered by high shrubs (*Salix*, *Hippophae* and *Betula*) interspersed with *Calamagrostis* and *Phragmites*. The field GP (*prativaga*) is sheltered only partly by the surrounding shrubs (*Salix*, *Hippophae*, *Phragmites*, *Calamagrostis*). The vegetation of both fields mainly consists of *Salix*, *Hydrocotyle*, *Carex* and



Graph 1c. The frequency distributions of the cephalothorax length of juveniles during the year.  
Subgroup *fulvipes*

*Parnassia*. This vegetation is mown yearly. Thus the habitats of both populations consist of a high (more than 70 cm) loosely structured vegetation surrounding a low (10–20 cm) densely grown over habitat. The spiders occurred especially in the transitional area. In spring juveniles were found mainly on the mown field. In autumn both adults and juveniles occurred in the surrounding shrubs.

The field BW (*pratavaga*, *pullata*) also is yearly mown. It is surrounded by trees and shrubs (*Betula*). The vegetation consists of *Lysimachia*, *Hydrocotyle*, *Carex* and moss (*Polytrichum*). In spring this vegetation is rather low (10 cm) and interspersed with bare ground. In summer the *Lysimachia* has grown up to 40 cm, and thus a loosely structured vegetation occurs. The spiders were found all over the mown field.



The above mentioned habitats are very wet during spring and autumn. The population VZ (*prativaga*) occurs in a rather dry area throughout the year. This area is situated on the border of dunes and arable land and is surrounded by trees (*Fagus*, *Quercus*, *Populus*). The vegetation consists of *Carex*, *Calamagrostis*, *Urtica* and *Cirsium*. In spring juveniles mainly occurred on the flattened grass. Adults and, in autumn, juveniles could be found in the loosely structured *Urtica* and *Cirsium* vegetation (height up to 40 cm).

The population Sch (*pullata*) occurs in a marshy dune meadow sheltered by shrubs and trees (*Alnus*). This yearly mown field is densely grown with *Hydrocotyle*, *Carex*, *Festuca* and moss carpets of *Polytrichum* and *Sphagnum* (15 cm). Especially in spring, autumn and winter this area is very wet; the spiders occurred throughout the area.

The population HR (*pullata*) occurs in a rather dry area surrounded by trees (*Pinus*). The area is densely grown with a moss carpet (*Polytrichum*) (10 cm) interspersed with tussocks of *Festuca* and *Calluna*.

The population AP (*pullata*) occurs in a yearly mown marshy area grown over with a moss carpet (*Polytrichum*, *Sphagnum*: 10 cm), *Carex*, *Iris*, *Hydrocotyle* and *Juncus* (30 cm). The area is very wet throughout the year. It is rather exposed in that it is not surrounded by trees and shrubs. As in the populations Sch and HR, both juveniles and adults occurred throughout the area.

Both the populations E and S (*fulvipes*) occur in fens sheltered by trees (*Pinus*, *Larix* and *Betula*). The vegetation of both areas consists of a moss carpet (*Sphagnum*, 10 cm) interspersed with tussocks of *Eriophorum* and *Erica*. The field in which population E occurs is more dry with more and larger tussocks of *Eriophorum* (40 cm) than the field of population S. The spiders occurred throughout the field both in the moss carpet and in the tussocks of *Eriophorum*.

## B. Conclusions

These data show that in general the habitats of the populations of the *P. pullata* group are wet fields sheltered by trees and shrubs. However, differences in soil moisture occur. The *fulvipes* populations (E and S) are found in the wettest habitats. Differences between the species exist in the structure of the habitat and in the behaviour of the spiders in the vegetation.

Populations of the *prativaga* subgroup (LP, BW, GP, VZ) occur in loosely structured, rather high vegetation with transitional areas. Adults remain low in the vegetation and motionless at low temperatures (ground temperature less than 15° C). With sunny, warm weather they walk through and over the plants. Juveniles (stage A-2 and stage A-1) show high locomotory activity in spring throughout the still undifferentiated vegetation. In autumn they (stage A-2) stay mainly in the dry layers of litter.

Populations of the *pullata* subgroup (BW, Sch, AP, HR) occur in densely structured, rather low vegetations, generally also including moss carpets. At low temperatures (less than 10° C) the spiders remain motionless in small spaces inside the vegetation. During warm, sunny weather they leave these spaces and walk upon the vegetation layer. Differences in behaviour in relation to the habitat are slight between juveniles (both in spring and in autumn) and adults.

The occurrence of populations of the *fulvipes* subgroup (E and S) is restricted to fens grown with a *Sphagnum* carpet. However, they occur in the densely structured moss carpet as well as in the loose tussocks of *Eriophorum*. The behaviour of the

Table V. Summary of the general differences and similarities between the studied subgroups of the *P. pullata* group.

Subgroup	<i>pratvaga</i>	<i>pullata</i>	<i>fulvipes</i>
final moult	5''	4''—4''' (5'')	5'
cocoon production	6'	5''	6'
egg maturing period	20 days	10—30 days	30 days
maximal numbers of ♂ ♂ and ♀ ♀	5'''	5'—5''	5'—5'''
copulation period	May	May	May
maximal numbers of ♀ ♀ c	6'''—7'	6'''—6'''	6'''—7'
emergence of first pulli	June	June	June
cocoon carrying period	20—30 days	30—40 days	20—30 days
length of reproduction cycle	50—60 days	45—75 days	60—70 days
number of cocoons	1	1 à 2	2 à 3
mean number of eggs per cocoon	40 à 50	30 à 40 (first roc) 20 à 30 (sec. coc)	30 (first cocoon) 20 (second cocoon) 10 (third cocoon)
variation	small	large	small
number of juvenile stages	6	6	6
mean ceph. length of the respective juvenile stages (MU)	20 (pulli), 26, 33, 40, 47, 55 (subadult)		
mean ceph. length of adults (MU) ♂ ♂ ♀ ♀	60—65 60—70	60—65 60—65	55—60 55—60
juv. stages in October	stage A-2	A-2, A-1	A-4, A-3, A-2, A-1
juv. stages in January	stage A-2	A-2, A-1	A-4, A-3, A-2, A-1
juv. stages in April	stage A-2, A-1	A-2, A-1	A-3, A-2, A-1
juv. stages in July	—	—	A-3, A-2

spiders of this subgroup in relation to habitat structure is comparable with that of the *pullata* subgroup (moss carpet) as well as with that of the *pratīvaga* subgroup (*Eriophorum* tussocks). However, under unfavourable weather conditions adults and especially juveniles show higher locomotory activity throughout the year than both *pullata* and *pratīvaga*.

#### IV. GENERAL CONCLUSIONS AND DISCUSSION

The results with respect to the phenology of the species of the *P. pullata* group are summarized in Table V. These results agree very well with the data given by Dahl (1908), Palmgren (1939), Wiebes (1959) and Vlijm & Kessler-Geschiere (1967). Generally the final moult occurs in spring (April, May) in the three subgroups of the *P. pullata* group. During May the numbers of males and females are highest, indicating that the period of copulation then occurs. At the end of May and the beginning of June the females produce their cocoons. In the same period the males disappear from the populations. Pulli emerge from the cocoons at the end of June and the beginning of July. They moult six times before the adult stage is reached. Between every moult, until the subadult stage is reached, the juveniles grow about 0.3 mm in cephalothorax length from 0.84 mm in the pulli stage to 2.31 mm in the subadult stage. The cephalothorax length of adult males and females is different in the three subgroups (Den Hollander, 1970).

Some differences in phenology exist between the three subgroups of the *P. pullata* group (Table V). These differences mainly concern the period in which the final moult occurs and the growth of juveniles in relation to the period in which they emerge from the cocoons. In general both males and females of the *pullata* subgroup moult to adult earlier in spring (about 20 days) than those of the subgroup *fulvipes*; in the subgroup *pratīvaga* the final moult occurs about 10 days later than in the subgroup *fulvipes*. However, cocoon production occurs at about the same time in the three subgroups (second half of May). Thus the egg maturing period, measured from the moment in which the first adult females can be found till the moment in which the first females produce a cocoon, is longer in the *pullata* subgroup than in both other subgroups.

Even when the final moult occurs later, as happens in some populations in the *pullata* subgroup in some years, the females produce their cocoons at about the same time. Thus dependent on the period in which the final moult occurs the length of the egg maturing period varies in the *pullata* subgroup from 10 to 30 days (*pratīvaga*: 10—20, *fulvipes*: 20—30 days). The cocoon carrying period is longer in the subgroup *pullata* than in both other subgroups (30—40 days and 20—30 days, respectively). This means that the period between the appearance of the first adults and the emergence of the first pulli from the cocoons (i.e. one reproduction cycle) is different in the three subgroups. Generally this period is shortest in the *pratīvaga* subgroup (50—60 days). In the subgroup *fulvipes* this period lasts 60—70 days. The reproduction cycle is short (45 days) or long (75 days) in the subgroup *pullata*, dependent on the time of the final moult (the later the final moult occurs, the shorter this period lasts). Adult males disappear from the populations in the beginning of June in the three subgroups. Because subadult males moult to adult earlier in the *pullata* subgroup than in the other subgroups; the length of the period that males occur in the populations, is longest in this subgroup, but is variable in relation to the time of the final moult. In the *pratīvaga*



subgroup this period normally is shorter than that in both other subgroups. Richter c.s. (1971) also found that, under laboratory conditions, the reproduction cycle of *P. prativaga* was shorter than that of *P. pullata*. Because the number of eggs in cocoons of *prativaga* is larger than in *pullata*, *P. prativaga* produces a larger number of offspring in a shorter period than *P. pullata*. Richter c.s. (1971) discussed these results in the context of the abundance of the habitats and the use of the habitats by the two species. *P. prativaga* should occur in rather specific habitats and this species might make a differential use of its habitat. This means that *P. prativaga* may be considered as a stenotopic species, *P. pullata* on the other hand would be an eurytopic species. However, *P. prativaga* var. *fulvipes* can be found only in fens with a *Sphagnum* carpet (Dahl, 1908; Holm & Kronestedt, 1970). Thus it may be considered a very stenotopic species. Nevertheless, the first reproduction cycle is longer than that in the subgroup *prativaga* and the egg sacs contain considerably less eggs. The length of its reproduction cycle may even be longer than that in the subgroup *pullata* and the number of eggs per cocoon is slightly lower than that in the *pullata* subgroup. Moreover, the mentioned laboratory experiments have not shown the variable length of the reproduction cycle in the *pullata* subgroup which sometimes even may be as short as that in the subgroup *prativaga*. However, in this context the microclimatic conditions of the habitat used by the respective species may be important.

Generally, the populations of the *P. pullata* group occur in two types of habitats. These habitats are characterized by a loosely structured, rather high (50 cm) vegetation on the one hand (*prativaga*) and a densely structured, rather low (15 cm) vegetation on the other hand (*pullata*, *fulvipes*). As a consequence of these different structures the characteristics of the microclimate vary between these habitats (Geiger, 1961). In the high vegetation a rather stable microclimate occurs. This microclimate is stabilized with regard to macroclimate at slightly lower temperatures and higher humidities. The microclimate in the low vegetation is very unstable. At sunny, calm weather both temperature and humidity of the microclimate are higher than those of the macroclimate. However, these conditions change quickly when wind velocity increases and the weather is clouded. Especially in spring the microclimate in the low vegetation is unstable because weather conditions vary in that time to a large extent. Thus, in the high vegetation a rather moderate stabilized microclimate occurs. On the contrary, in the low vegetation extreme conditions occur, dependent on the weather.

These microclimatological features may relate to the phenological characteristics of the species. The instability of the microclimate in the habitat of the populations of the subgroup *pullata* (low vegetation) may be related to the variations in the period in which the final moult occurs, both between populations and between the successive years. Inter-population variation of phenological data was larger in 1970 than in 1969. In addition, in most populations the final moult occurred later in 1970 than in 1969. Indeed, weather during the spring was very different in these years. In April 1970 there was 26% less sunshine than in 1969. Probably, the differences in the period of the final moult between the respective populations of the *pullata* subgroup are caused by differences in the structure of their habitats.

The microclimate in the habitat of the populations of the subgroup *prativaga* (high vegetation) is rather stable. Indeed, the final moult occurred very synchronized in the respective populations and in the same period in the successive years. The habitat of the populations of the *fulvipes* subgroup is to some extent intermediate between that of the



*prativaga* subgroup and that of the *pullata* subgroup. Both high and low vegetations occur in this habitat. Although the number of populations studied is too small for a clear conclusion, the final moult in the *fulvipes* subgroup seems to be less synchronized than that in the *prativaga* subgroup, but more synchronized than that in the *pullata* subgroup.

As most phenological characteristics relate to the period in which the final moult occurs, they are influenced by the microclimatological characteristics. Thus it seems plausible that variations in phenological characters of the species in the *P. pullata* group are related to the type of habitat in which they occur.

In this context the growth of juveniles is important. In the *prativaga* subgroup pulli emerge from the cocoons in the beginning of July only. They grow and overwinter as stage A-2 juveniles. Next spring they moult to subadult and adult (Graph 2a).

In the *pullata* subgroup pulli emerge from the cocoons in the second half of June (first cocoon) and in the second half of July (second cocoon), these juveniles overwinter as stage A-1 juveniles (first cocoon) and stage A-2 juveniles (second cocoon). (Graph 2b).

In the *fulvipes* subgroup females produce three cocoons in succession. Pulli emerge from these cocoons in the beginning of July (first cocoon), the beginning of August (second cocoon) and in the beginning of September (third cocoon), respectively. The juveniles which have emerged from the first cocoons grow to the adult stage as juveniles in the subgroup *prativaga* do. Those which have emerged from the second and third cocoons, however, overwinter twice before the final moult occurs. The first overwintering occurs during stage A-3 and stage A-4 for juveniles emerged from the second and third cocoons, respectively. The second overwintering takes place during stage A-1 (subadult) for both categories of juveniles (Graph 2c).

These results show that only juveniles which overwinter during the last two instars before the adult stage moult to adults next spring. Laboratory experiments (unpublished results) have shown that a period of low temperatures is necessary to induce the final moult. The present results show that such an induction only can occur during the last two instars before the final moult. Probably endocrine processes have to be started by a period of low temperatures during this developmental stage (Eckert, 1967; Streble, 1966). When these processes have been started the juveniles moult once or twice in succession to become adult during spring. In the other case they moult only once and occur in this stage in the populations during the summer. However, juveniles in the *pullata* subgroup normally moult to adult earlier in spring than juveniles in both other subgroups. Probably an external factor induces the time of the final moult. Temperature may be this factor. If this is true, then it may be concluded that the final moult in the *pullata* subgroup is already induced at lower temperatures than in the subgroup *prativaga* and *fulvipes*.

The numbers of eggs produced per female are rather similar in the three subgroups (*prativaga*: 47; *pullata*: 44, *fulvipes*: 55). However, this number is produced in the *prativaga* subgroup in one egg batch, whereas in the *pullata* subgroup this number is produced partly in two egg batches and in the *fulvipes* subgroup in three egg batches. This phenomenon may represent a mechanism of spreading of the risk (Den Boer, 1968). The habitat of *P. prativaga* var. *fulvipes* is very unstable, that of *P. prativaga* is rather stable. Thus *P. prativaga* var. *fulvipes* produces the total number of eggs in

three periods, *P. prativaga* in one period. The stability of the habitat of *P. pullata* is about intermediate: the total number of eggs is produced in one or two periods.

Using the classification of Southwood (1962) and Johnson (1969), Richter (1970) mentioned the habitat of *P. pullata* as abundant with intermediate stability. The habitat of *P. prativaga* would be rare and unstable. The same seems to be true for *P. prativaga fulvipes* to a larger extent. However, no clear relations seem to exist between the total number of eggs produced per female, in one, two or three egg batches, and the abundance and stability of the habitat.

The above mentioned results also may be discussed in the context of the classification of the species in the *P. pullata* group. Dahl (1908), Simon (1932), Wiebes (1959), Tongiorgi (1966) and Holm & Kronstedt (1970) describe various species and subspecies within the *P. pullata* group. This division is mainly based on small differences in the structure of the external genital organs, the annulation and spinosity of the legs and the size and colour of the specimens. However, Den Hollander (1970) has shown that some of these characters vary to a rather large extent, both within and between populations of the same species (*P. pullata*, *P. prativaga* and *P. prativaga* var. *fulvipes*). He also suggests the occurrence of hybridization in mixed populations of *P. pullata* and *P. prativaga*. Indeed, under laboratory conditions, intermediate specimens have been obtained from males of *P. prativaga* and females of *P. pullata* (Den Hollander, in preparation). Thus the distinction between the various species and subspecies of the *P. pullata* group seems to be rather doubtful. Indeed, the phenological differences between the species studied by me are rather small. Rather large variations could be shown between populations of the same species (*P. pullata*). Probably the phenological differences as well as the variation of phenological characteristics may relate to specific characteristics of the habitats used by the respective species.

On the other hand, various species of the *P. pullata* group occur in mixed populations. In France mixed populations of *P. pullata* and *P. prativaga*, *P. pullata* and *P. femoralis*, and of *P. prativaga* and *P. femoralis* have been observed. In the Netherlands mixed populations of *P. prativaga* and *P. pullata*, and of *P. pullata* and *P. prativaga* var. *fulvipes* occur (Den Hollander, 1970, and unpublished results). Thus the differences between the species may also result from a differential use of the habitat by the respective species. The evolution of the *P. pullata* group seems to be such that various species have originated which at present can be mainly separated only by their ecological characteristics. The development of morphological, ethological and physiological differences seems to be in progress (ecological speciation, Grant, 1963).

It should, however, also be mentioned that populations of the *P. pullata* group may have been isolated geographically from each other, e.g. during ice-ages. During this time of isolation characters may have been acquired which promote or guarantee reproductive isolation when the external barriers break down (Mayr, 1942). In the case of the *P. pullata* group, the development of these characters may be, as yet, incomplete.

Whatever the mechanisms of speciation (ecological or geographical) may have been, the various species have been adapted to special types of habitat. As a consequence, isolating characters have been evolved.

Further studies concerning these problems are necessary for further evaluation of the relations between the species of the *P. pullata* group.

The occurrence of hybridization between closely related species in mixed populations may be prevented by several mechanisms (Mayr, 1969). Mating between males and

females of different species, may be prevented by seasonal or habitat isolation, ethological isolation and mechanical isolation. The results of the present study deal with the occurrence of seasonal isolation in mixed populations of *P. prativaga* and *P. pullata*. Preliminary laboratory experiments have shown that ethological and mechanical barriers do not exist between males of *P. prativaga* and females of *P. pullata*. Ethological barriers seem to prevent mating of males of *P. pullata* with females of *P. prativaga* (cf. Den Hollander, in preparation).

The results of this phenological study have shown that males of *P. pullata* and receptive females of *P. prativaga* normally occur together in mixed populations. The reversed combination of males and females does not occur. Thus in mixed populations the species *P. prativaga* is isolated from the species *P. pullata*, partly by seasonal barriers and partly by ethological barriers. However, the seasonal barriers can be broken down by cold weather during spring. Then the final moult in *P. pullata* is postponed and males of *P. prativaga* occur together in the populations with receptive females of *P. pullata*. Generally, the two species use a different type of habitat. Indeed, even in mixed populations they seem to use different parts of the habitat. However, this is especially true for females carrying cocoons, while females without cocoons, i.e., receptive females, as well as males seem to use the habitat less differentially (Den Hollander & Lof, in preparation). These results show that habitat isolation, seasonal isolation, as well as ethological isolation, exist between the species concerned but that each of these barriers seems to be incomplete. Thus hybridization in mixed populations between males of *P. prativaga* and females of *P. pullata* may occur when, because of the weather conditions in spring, the final moult in *P. pullata* is postponed till the beginning of May.

**Postscript.** According to Mr. Kronestedt who kindly studied a number of specimens of each of the investigated populations, the form *P. prativaga* var. *fulvipes* (Collett, 1875) correctly should be named *P. sphagnicola* (Dahl, 1908). (Holm & Kronestedt, 1970).

## V. SUMMARY

1. Ten populations of the *Pardosa pullata* group (*P. prativaga*: 4; *P. prativaga* var. *fulvipes*: 2; *P. pullata*: 4) were sampled once every ten days from April till September in 1969 and 1970.

2. The numbers of juveniles, adult males and females (the last with and without cocoon) in every sample were established. The length of the cephalothorax of the juveniles in every sample was measured. On the basis of these data the phenology of the species of the *P. pullata* group was studied.

3. Generally the final moult occurs earlier in spring in *P. pullata*, than in both *P. prativaga* and *P. prativaga* var. *fulvipes*. However, the time of the final moult varies in *P. pullata* per population and per year.

4. First cocoon production occurs in about the same period in the studied populations in both years.

5. In *P. prativaga* females normally produce a cocoon only once; in *P. pullata* they produce a cocoon once or twice, and in *P. prativaga* var. *fulvipes* the females produce two or three cocoons in succession.

6. The development of juveniles from pulli to the adult stage is somewhat different in the different species.

7. The numbers of eggs per cocoon in *P. prativaga* are larger than those in both *P. pullata* and *P. prativaga* var. *fulvipes*. When females produce two or more cocoons in succession, the number of eggs per cocoon is about 40% lower in each following egg batch.

8. The differences in the period in which the final moult occurs in populations of the *P. pullata* group are discussed in the context of microclimatological characteristics of the habitat.

9. As yet, no clear relationships seem to exist between the total number of eggs produced per female, in one, two or three egg batches, and the abundance and stability of the habitats.

10. The phenological data have been discussed in the context of the classification of the *P. pullata* group as well as in the context of the possibility of the occurrence of hybridization in mixed populations.

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